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The Stromatoporoid Genera *Actinostroma* Nicholson and *Nexililamina* gen. nov. from the Devonian Broken River Formation, North Queensland

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Abstract: Five species of *Actinostroma*, including one new species *A. steloges*, are described, from Middle Devonian Members of the Broken River Formation. Specimens of *A. clathratum* Nicholson and *A. papillosum* are distinguished by considering the number of pillars and laminae measured in 5 mm, and the gallery index of specimens. *Nexililamina* gen. nov. is proposed to embrace species with laminae composed of thin sheets of compact tissue, which may in places combine to form complex laminae. The type species of the new genus is *N. dipcreekensis* sp. nov.

INTRODUCTION

Stromatoporoids are common in the limestone members of the Broken River Formation on Pandanus Creek Station, Shield Creek Holding, North Queensland. The Collection area is situated approximately at latitude 19°13'S. and longitude 144°45'E.

Most of the fossils described are from the Chinaman Creek Limestone Member and the Dip Creek Limestone Member (Jell 1968) of the Broken River Formation, with a few specimens from isolated rudites within the Broken River Formation. Fossils are stored in the School of Geology and Mineralogy, University of Queensland, and are catalogued with University Fossil Numbers (e.g. F.47607) and Fossil Locality Numbers (e.g. L.2979). A description of each fossil locality is given in Appendix.

Subgeneric Divisions of Actinostroma

Ripper (1938) divided the species of *Actinostroma* into three groups, based on the structure of the laminae and the continuity of pillars. Lecompte (1951) described five groups of species, but he included only those forms found in the Middle and Upper Devonian of the Ardennes, Belgium. Flügel (1959) in his review of the genus considered all described species of *Actinostroma*, and arranged them in eight groups within two subgenera. Nestor (1964) erected the genus *Plectostroma* Nestor, to include those species of *Actinostroma* grouped with *A. intertextum* Nicholson by Flügel and characterized by thin discontinuous laminae.

Most of the specimens described here can be arranged in two of the species groups proposed by Ripper, Lecompte and Flügel. The group of *A. stellulatum* Nicholson is characterized by specimens with well-developed laminae, long pillars, rectilinear galleries, and usually more than seven pillars and laminae in 1 mm. This group is represented by the nominate species only. The second group is *A. clathratum* Nicholson, characterized by well-developed laminae, long pillars, rectilinear galleries, and usually fewer than 5 laminae and pillars per mm. Representatives of this group are *A. clathratum*, *A. papillosum* (Bargatzky), and *A. dehornae* Lecompte. *A. steloges* sp. nov. does not conform to any of the proposed groupings. The group of *A. verrucosum* proposed by Lecompte is represented, and is described as a new genus, *Nexililamina*.

SPECIATION

Workers have used many different features as specific characters in *Actinostroma*, but Flügel (1959) rejected all criteria except the structure and spacing of the laminae and pillars. He used 'Art diagram' and 'Art feld' to define numerically and graphically the variation in the number of pillars and laminae in 1 mm of a vertical section of a stromatoporoid coenosteum. Extreme variants are eliminated by the use of the 'maximum', which includes all values of the 'art diagram' that occur at least twice in ten measurements. For example,

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if ten measurements gave values 3, 4, 4, 5, 5, 5, 5, 6, 6, 7 the 'maximum' is [4-6]. The 'maximum' describes limits within which most of the measurements of a species lie. The method of Flügel for defining species has not been used, as the small number of pillars and laminae in 1 mm mask the differences between and within coenostea.

Klovan (1966) introduced a new index to aid in distinguishing species, the gallery index, which is the average ratio of the heights of galleries to their lengths. The gallery index may be measured directly, or calculated from the thickness and spacing of the pillars and laminae.

In most cases, species of *Actinostroma* are readily identified by measuring the distribution of pillars and laminae, which yield clear groupings of values corresponding to species. With the species *A. dehornae, A. papillosum* and *A. clathratum*, this is not possible. The arrangement of pillars and laminae in all species appears similar, and the variation in the spacing of the skeletal elements of *A. papillosum* overlaps that of *A. dehornae*, and falls within that of *A. clathratum*.

Lecompte (1951) stated when he proposed *A. devonense* (= *A. papillosum*) that it could be distinguished from *A. clathratum* by the spacing of the pillars. Flügel (1959), however, considered that the two species could be distinguished by the spacing of laminae rather than pillars. All workers have distinguished *A. dehornae* on the basis of the widely spaced laminae, which are also differentiated in zones, closely and distantly spaced.

In separating the species of this collection, dimensions of fossils were determined, to see if one or a combination of characters could provide a guide to speciation. Commonly ten measurements were taken of each character in each coenosteum. The characters measured were: number of laminae in 5 mm vertical section, number of pillars in 5 mm vertical section, number of pillars in 1 mm² tangential section, thickness of laminae, diameter of pillars, and (calculated from these) the gallery index of Klovan (1966). The results of these measurements have been synthesized and are reported in the descriptions of the species. Data for each character are given in the following form:

M = The mean value of all measurements taken in each species (equal number of measurements in each specimen).

σM = The standard deviation of the mean values of individual coenosteum, from the overall mean of the species.

σm = The average of the standard deviations within coenostea from their respective means.

When these measurements were obtained, it was clear that there were present in the collection specimens which could be allocated to *A. dehornae*, *A. papillosum*, and *A. clathratum*. All the mean values for individual coenostea were plotted on 'pillars in 5 mm versus laminae in 5 mm' and 'pillars in 1 mm² versus laminae in 5 mm' graphs, but no obvious separation of species resulted. The values of the gallery indices for the specimens were then superimposed on these plots. It was possible to divide the collection into groups with characteristic gallery index curves on the pillar/laminar plots. This allowed a distinction to be drawn between specimens with the same distribution of pillars and laminae, but whose gallery index differed because of different thicknesses of pillars and laminae. These differences could not commonly be detected qualitatively, and required measurements to be made for them to be established.

SYSTEMATIC DESCRIPTIONS

Genus **Actinostroma** Nicholson 1886

Actinostroma Nicholson 1886, p. 75; Ripper 1937, p. 12; 1938, p. 222; Flügel 1959, p. 123; Stearn 1966, p. 86.

Type Species: *Actinostroma clathratum* Nicholson 1886, p. 76, Pl. 1, fig. 11-13; 1886a, p. 226, Pl. 4, fig. 1-3, from the Middle Devonian (Givetian of Gerolstein, West Germany).

Diagnosis: Coenostea are composed of well-developed laminae and pillars. Pillars are continuous and traverse many laminae. Laminae are composed of arms which radiate from the pillars and unite to form an hexactinellid network, which is usually apparent in tangential section. Tissue is compact. Astrorhizae and dissepiments are present.

Range: *Actinostroma* is known from the Lower Silurian of Europe, Middle and Upper Silurian of Europe, Asia, and North America, and is cosmopolitan in the Devonian.

Actinostroma dehornae Lecompte

(Pl. 13, fig. 3, 5)

A. dehornae Lecompte 1951, p. 96, Pl. 4, fig. 1-4; Zukalová 1958, p. 319, Pl. 2, fig. 1-2; Flügel 1959, p. 140, Pl. 7, fig. 1.

Holotype: Specimen number 4136 in Lecompte's collection in The Royal Institute of Natural Sciences, Brussels, collected from the Upper Devonian, Frasnian of Surice, Belgium.

Diagnosis: Coenostea are globular and may have well-developed latilaminae. Laminae are continuous, 0·05 to 0·10 mm thick, and the average number in 5 mm for each coenosteum generally ranges from 10 to 20. The laminae are irregularly zoned and are arranged in zones of greater and lesser density. The diameter of the continuous pillars ranges from 0·10 to 0·20 mm, the average number in 5 mm for each coenosteum ranges between 10 and 20, and the aver-

age number in 1 mm² ranges from 7 to 11. The gallery index lies between 1·0 and 1·5.

DESCRIPTION OF BROKEN RIVER SPECIMENS: Coenostea are globular. The tissue is melanospheric or flocculent, sometimes with dark-coloured axial zones in the laminae.

In vertical section laminae are continuous, with the thickness means for the coenostea ranging from 0·05 to 0·07 mm (M = 0·057, σM = 0·009). The laminae undulate gently but irregularly, and are irregularly spaced. The surfaces of some specimens show a zonation which corresponds to areas in the coenostea where laminae are more closely or more distantly spaced. These zones average 1 mm in width and the numbers of laminae in 1 mm can be as low as 3 where they are distantly spaced, or 8 where they are closely arranged. The zones are not present in all specimens and are weakly developed in others. The average number of laminae in 5 mm for each coenosteum ranges from 19 to 21 (M = 19·9, σM = 0·8, σm = 1·1). Pillars are continuous and straight, with an average diameter for each coenosteum ranging from 0·10 to 0·17 mm (M = 0·123, σM = 0·025). The average number of pillars in 5 mm varies between 12 and 14 (M = 13·0, σM = 0·58, σm = 0·84). Laminae are upturned around occasional astrorhizal systems, which average 6 mm in diameter. Galleries are rectangular, show very little rounding at the corners, and have a gallery index of from 1·3 to 1·5 (M = 1·44, σM = 0·08).

In tangential section, circular cross-sections of pillars are joined by faint arms in an hexactinellid network, where laminae are intersected. The arms are usually destroyed by recrystallization. The average number of pillars in 1 mm² for each coenosteum ranges from 8 to 11 (M = 8·8, σM = 0·78, σm = 0·71). There are five specimens in the collection.

REMARKS: Lecompte (1951) justified the erection of this species by the irregularity of the laminae and their tendency to be arranged in groups more closely and more distantly spaced. The Broken River specimens agree well with the holotype of the species in the degree of development and distribution of pillars and laminae, but the grouping of laminae in more closely and more distantly spaced bands is less pronounced (see Pl. 13, fig. 5).

A. dehornae has fewer pillars in 5 mm and 1 mm² than either *A. clathratum* or *A. papillosum*, and specimens of it have higher gallery indices than both other species. When the gallery indices are contoured on a pillar laminar plot, they show a continuation of the values of *A. clathratum*, and are much higher than those of *A. papillosum*. This suggests that *A. dehornae* and *A. papillosum* have both arisen from a common ancestor, *A. clathratum*. Specimens were assigned to *A. dehornae* if the average number of pillars was less than approximately 14 in 5 mm and 11 in 1 mm² and the gallery index 1·3 or more.

RANGE: The species has been reported from the Frasnian of Belgium (Lecompte 1951), and Givetian and Frasnian of Czechoslovakia (Zukalová 1958, and Dvorák, Chlupac & Svoboda 1958). It was found in the Chinaman Creek Limestone Member of the Broken River Formation, on the traverse along Chinaman Creek South, 500 m upstream from the base of the Member (L.2510).

Actinostroma clathratum Nicholson

(Pl. 13, fig. 2, 4)

Actinostroma clathratum Nicholson 1886, p. 76, Pl. 1, fig. 11-13; Lecompte 1951, p. 77, Pl. 1, fig. 1-12 Flügel 1959, p. 129.

LECTOTYPE: Specimen No. 141/P.5774 in the British Museum (Natural History) illustrated by Nicholson (1886, Pl. 1, fig. 11), selected by Schouppé (1954, p. 431), and collected from the Middle Devonian of Gerolstein, West Germany.

DIAGNOSIS: Coenostea are globular, encrusting or laminar. Laminae and pillars form a regular network with pillars usually thicker than laminae. Pillars are long, with a diameter of approximately 0·06 to 0·12 mm, and the average number in 5 mm in vertical section usually ranges between 20 and 25. Strong continuous laminae are generally 0·04 to 0·12 mm thick, and the average number in 5 mm for each coenosteum usually lies between 20 and 25. In tangential section there are usually 15 to 28 pillars in 1 mm².

DESCRIPTION OF BROKEN RIVER SPECIMENS: Coenostea are globular, laminar, or encrusting. Low undulations are present on the surface, but no well-developed mamelons are present. In rare specimens where the tissue is well preserved, the laminae and pillars are composed of yellow compact tissue, which is, however, commonly altered to a melanospheric or flocculent condition.

In vertical section laminae are continuous, evenly curved and spaced, with the mean thickness for the coenostea ranging from 0·03 to 0·07 (M = 0·054, σM = 0·012). The average number in 5 mm for each coenosteum ranges from 13 to 28 (M = 21·0, σM = 2·7, σm = 1·2). Pillars are long and continue through many laminae with an average diameter varying from 0·06 to 0·12 mm (M= 0·10, σM = 0·019). The average number in 5 mm ranges between 15 and 28 (M = 20·0, σM = 2·9, σm = 1·1). Galleries are rounded at their corners and the mean calculated gallery index for the collection is 0·90 (σM = 0·23). The value of the gallery index corresponding to the number of laminae and pillars is shown in Fig 1 and 2. Thin, curved dissepiments are present in the galleries.

In tangential section laminae occur as perforated sheets of tissue or as dense hexactinellid networks, depending on the degree of alteration. Pillars are roughly circular in cross-section. The average number of pillars in 1 mm² ranges between 11 and 28 (M = 17·8, σM = 4·9, σm = 1·0). Thin, curved dissepiments in places join pillars. Astrorhizae average 5 mm in diameter and their centres are 8 mm apart; the astrorhizae have groups of axial canals approximately 0·09 mm diameter. There are 25 specimens in the collection.

REMARKS: Specimens of *A. clathratum* which have a

similar number of laminae and pillars in 5 mm to *A. papillosum* are distinguished by higher gallery indices (i.e. more horizontally elongated galleries). This can be seen by comparing Fig. 1 with Fig. 3. These show the change in the value of the gallery index with the change in the numbers of pillars and laminae in 5 mm and 1 mm², for *A. clathratum* and *A. papillosum*. The use of Fig. 1-4 in separating specimens into *A. clathratum* and *A. papillosum* is illustrated by comparing the values of the gallery index in both species for 15 pillars and 20 laminae in 5 mm in vertical section. The value for *A. papillosum* is 0·95 (see Fig. 3) and 1·25 for *A. clathratum* (Fig. 1). The differing gallery index for corresponding numbers of pillars and laminae separates the two species over most of the range of variation in the species; however, where the value of the gallery index is around 0·9, and the number of laminae in 5 mm is less than twenty, it is difficult to place the specimen confidently in either species.

No detailed measurements of the characters of the lectotype, and the rest of Nicholson's original collection in the British Museum (Natural History) have been published, but Lecompte (1951) listed generalized measurements. From these measurements the gallery indices were calculated, and the specimens compared with this collection. The lectotype of *A. clathratum* (see Fig. 1 and 2) has more closely spaced pillars and laminae than most of the specimens in this collection, and the gallery index is higher. This may be the result of inadequate data. When Nicholson's collection in the British Museum (Natural History) is examined (based only on Lecompte's data) according to the criteria outlined above, Nos. 141 (Lectotype), 142, 144, 145, 150, 151, and 154 are allocated to *A. clathratum*, and Nos. 148, 149 and 153 to *A. papillosum*.

RANGE: Flügel (1959) reviewed the literature concerning this species, and concluded that it occurs most commonly in the Givetian and the Frasnian, but also is present in the Couvinian. The species is very widespread, and is reported from England, Belgium, Germany, Italy, North Africa, U.S.S.R., Czechoslovakia, Southwest China, and Western Australia (Flügel and Flügel-Kahler 1968). In the Broken River Formation this species is found throughout the Chinaman Creek Limestone Member along Chinaman Creek South (L.2509, L.2510, L.2976), and from 150 m SW. of the base of the Dip Creek Limestone Member, to its top, on the Martin's Well traverse, 1 km SW. of Martin's Well (L.2978, L.2980, L.2984).

Actinostroma papillosum (Bargatzky)

(Pl. 13, fig. 1)

Stromatopora papillosa Bargatzky 1881, p. 281.
A. clathratum var. 2 and var. 3 Nicholson 1889, p. 131, Pl. 12, fig. 2-3.
A. devonense Lecompte 1951, p. 88, Pl. 2, fig. 3-6, Pl. 3, fig. 1-3.
A. papillosum (Bargatzky); Flügel 1959, p. 167.

LECTOTYPE: Selected by Flügel (1959): *Stromatopora papillosa* Bargatzky (1881), specimen number 5 in Bargatzky's collection, Museum of the Institute of Geology and Palaeontology, University of Bonn, collected from the Givetian of 'Sehladetal', Paffrath-Mulde, West Germany, illustrated by Lecompte (1951), Pl. 1, fig. 11.

DIAGNOSIS: Coenostea are globular or laminar, and latilaminae may be present. Laminae are continuous,

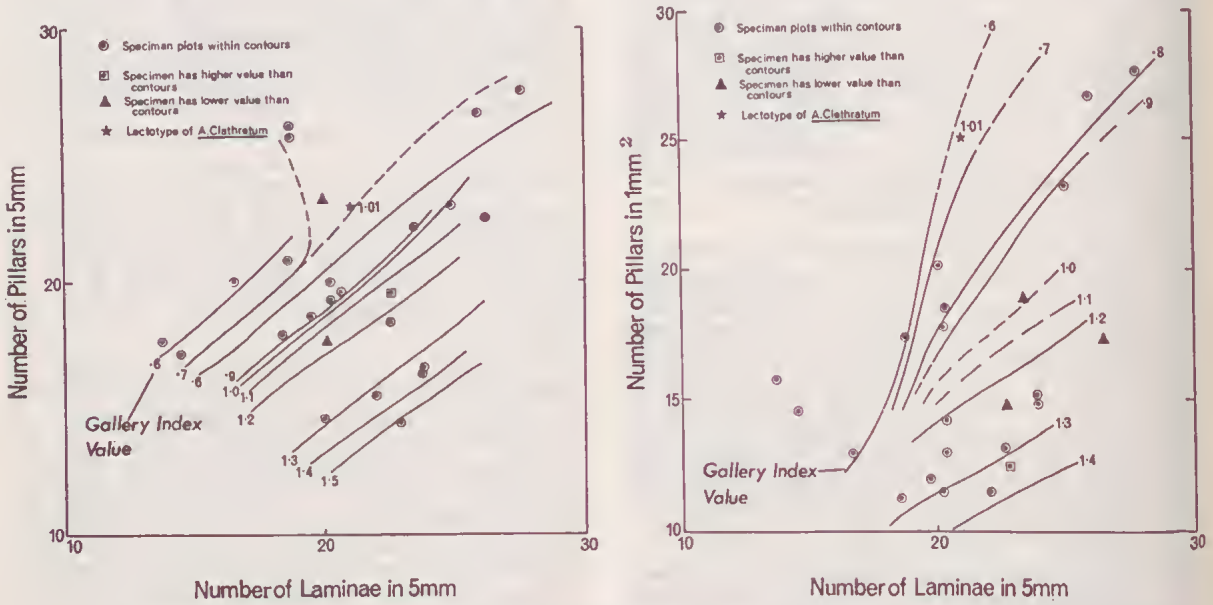

FIG. 1, 2—The variation of gallery index with the distribution of pillars and laminae in *A. clathratum* Nicholson.

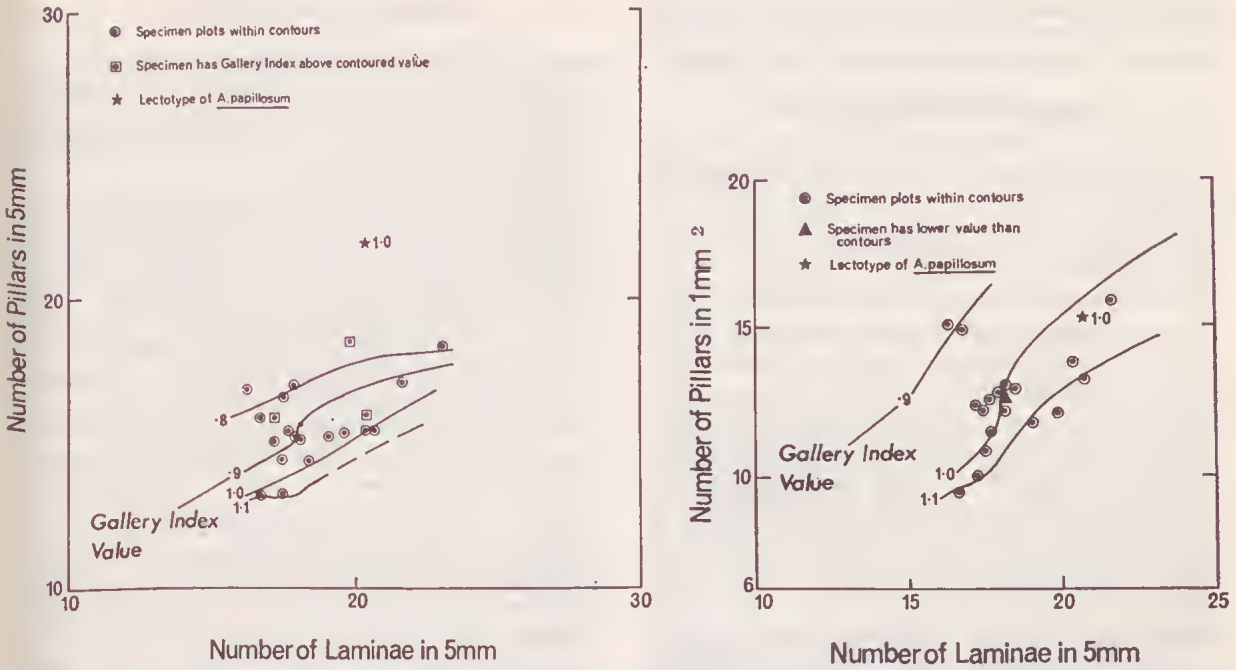

FIG. 3, 4—The variation of gallery index with the distribution of pillars and laminae in *A. papillosum* (Bargatzky).

usually 0·03 to 0·10 mm thick, with the average number in 5 mm generally between 15 and 23, and they may be irregularly spaced in some places. Pillars are long and continuous, with a diameter of approximately 0·08 to 0·12 mm, and the average number in 5 mm usually ranges from 15 to 25. The average number in 1 mm² is commonly from 10 to 15. The gallery index is approximately 1.

DESCRIPTION OF BROKEN RIVER SPECIMENS: Coenostea are globular or laminar. The tissue is commonly flocculent or melanospheric and has formed from the alteration of the originally compact tissue.

In vertical section laminae are strong and continuous and range in thickness from 0·03 to 0·08 mm ($M = 0·052$, $\sigma M = 0·014$). The average number in 5 mm ranges from 16 to 23 ($M = 18·5$, $\sigma M = 1·4$, $\sigma m = 0·97$). Pillars are long and continuous with a diameter from 0·08 to 0·12 mm ($M = 0·11$, $\sigma M = 0·01$), and the average number in 5 mm ranges from 13 to 19 ($M = 15·7$, $\sigma M = 1·0$, $\sigma m = 0·9$). Galleries are slightly rounded at the corners and the average gallery index for the collection is 0·98 ($\sigma M = 0·09$).

In tangential section laminae are represented by areas where the hexactinellid network is prominently developed. Pillars are isolated in some areas of the sections, but the greater part of any slide is occupied by the hexactinellid network, where pillars are joined to their neighbours by 3 to 6 arms in a rigid pattern. Pillars are approximately circular in cross-section and the average number in 1 mm² ranges from 9 to 17 ($M = 12·7$, $\sigma M = 1·4$, $\sigma m = 0·88$). Obscure astrorhizal systems, 8 to 10 mm apart, consist of an axial canal with radiating branches. There are 22 specimens in the collection.

REMARKS: Lecompte (1951) reviewed Nicholson's collection of *A. clathratum* and equated *A. clathratum* var. 2 and 3 of Nicholson with a new species, *A. devonense* Lecompte. He considered that specimens described as *Stromatopora papillosa* by Bargatzky (1881) belonged to *A. clathratum* var. 1 of Nicholson, basing his conclusion on the number of laminae and pillars in 5 mm. Flügel (1959), in his review, considered that *S. papillosa* Bargatzky corresponded to *A. c.* var. 2 and 3, on the basis of the 'maximum' and that the specific name *papillosa* had precedence over *clathratum* and *devonense*. The position of the lectotype chosen for *A. papillosum* (Bargatzky) by Flügel is not clear. The numbers of pillars and laminae in 5 mm certainly seem very similar to the lectotype of *A. clathratum* s. str., but the numbers of pillars in 1 mm² given by Lecompte (1951) are much lower. The specimen has been plotted on Fig. 3 and 4 and it can be seen that it does not correspond well with the collection here assigned to *A. papillosum*; in fact it is very close to the lectotype of *A. clathratum* (see Fig. 1). In Fig. 4 there is much better agreement with the present collection. The lectotype needs more careful description before it can be definitely established as synonymous with *A. clathratum*. If the lectotype is maintained separate from *A. clathratum*, it is certainly at the limit of the species here assigned to *A. papillosum* for which Lecompte established *A. devonense*.

RANGE: *A. papillosum* is found only in the Chinaman

Creek Limestone Member of the Broken River Formation, from 500 to 1,000 m W. of the base of the Member on Chinaman Creek South (L.2510, L.2976).

Actinostroma stellulatum Nicholson
(Pl. 13, fig. 6, 7)

A. stellulatum Nicholson 1892, p. 231, Pl. 6, fig. 8-9; Lecompte 1951, p. 111, Pl. 11, fig. 1-5; Flügel 1959, p. 179 (*pars*).
A. stellulatum var. *maureri* Lecompte 1951, p. 118, Pl. 12, fig. 1-3.
A. perlaminatum Lecompte 1951, p. 120, Pl. 12, fig. 4.

HOLOTYPE: Specimen No. 170/P5570 in the British Museum (Natural History) London, collected from the Givetian of Gerolstein, West Germany.

DIAGNOSIS: Coenostea are globular or laminar and latilaminae may be present. Laminae are evenly curved and spaced, usually with an average of 28 to 35 in 5 mm. Pillars are straight and continuous, the average number in 5 mm generally ranges from 28 to 35. In 1 mm² in tangential section, the average number usually lies between 35 and 45. The gallery index is approximately 0·75.

DESCRIPTION OF BROKEN RIVER SPECIMENS: Coenostea are globular or laminar, some with large mamelons 12 mm apart and 5 mm high. Tissue is compact, but may have altered to a flocculent condition in parts of the coenostea.

In vertical section laminae are strongly developed with an average thickness of 0·05 mm, and the average number in 5 mm ranges from 24 to 32 ($M = 27·3$, $\sigma M = 2·6$, $\sigma m = 1·2$). Pillars are continuous and regularly spaced with an average diameter of from 0·06 to 0·08 mm ($M = 0·069$); the average number in 5 mm ranges between 28 and 33 ($M = 28·5$, $\sigma M = 0·8$, $\sigma m = 1·4$). Galleries are rounded at their corners and have an average gallery index of 0·73 ($\sigma M = 0·02$). Astrorhizae are not apparent, but in the axial regions of mamelons there are a few thin dissepiments.

In tangential section laminae are concentrically arranged around mamelons. Laminae are composed of perforated sheets of compact tissue in which radial arms 0·05 mm thick are in places developed. Pillars are round in cross-section and the number in 1 mm² ranges between 38 and 41 ($M = 39·4$, $\sigma M = 1·1$, $\sigma m = 1·9$). There are three specimens in the Broken River collection.

REMARKS: This species is distinguished from the other species of *Actinostroma* in the collection by the much larger number of pillars present in 1 mm² in tangential section.

RANGE: *A. stellulatum* has been described from Belgium, Germany, England, U.S.S.R., and North America, from strata ranging in age from Couvinian to Frasnian (see Flügel 1959: 185). In the Broken River Formation it occurs in the Dip Creek Limestone Member (Couvinian) on Dip Creek 2·4 km upstream from the junction of Dip Creek and Pandanus Creek (L.2499). It occurs also in isolated rudites (Couvinian?).

Actinostroma steloges sp. nov.
(Pl. 14, fig. 1-3)

HOLOTYPE: Fossil numbered F.47755 from the Couvinian Dip Creek Limestone Member of the Broken River Formation, 800 m SW. of the base of the Member, 1 km SW. of Martin's Well, Pandanus Creek Station, North Queensland.

DIAGNOSIS: Coenostea are globular with irregular low undulations, and latilaminae may be present. Laminae are 0·12 to 0·2 mm thick and are pierced by some large pores. There are from 9 to 14 laminae in 5 mm. Pillars are continuous and their diameter ranges from 0·22 to 0·28 mm, with from 9 to 13 in 5 mm. There are from 17 to 24 pillars in 4 mm² in tangential section. Galleries are rounded to subrounded, and the gallery index ranges from 0·5 to 1·0. Dissepiments occur in the galleries and astrorhizae are not present.

DESCRIPTION: The coenostea are discoidal or globular, with undulating laminae but no mamelons. Latilaminae are developed 5 mm apart. The tissue is compact, but rarely is fibrous in the laminae. In the holotype, the pillars have a dark lumen. It is possible that there has been slight alteration and that these types of tissues have developed from an originally compact tissue.

In vertical section laminae are commonly continuous, slightly irregularly spaced, and they range in thickness from 0·12 to 0·20 mm ($M = 0·16$, $\sigma M = 0·02$). In some areas the laminae appear to be discontinuous, and are replaced by thin dissepiments. The average number of laminae in 5 mm for each coenosteum ranges from 9 to 14 ($M = 12·3$, $\sigma M = 1·4$, $\sigma m = 0·75$). Pillars are continuous, and the average number in 5 mm ranges from 9 to 13 ($M = 10·6$, $\sigma M = 0·95$, $\sigma m = 0·76$). The average pillar diameter for coenostea ranges from 0·22 to 0·28 mm ($M = 0·25$, $\sigma M = 0·02$). Galleries are rounded to subrounded, 0·16 to 0·23 mm high, and have an average gallery index from 0·5 to 1·0 ($M = 0·80$, $\sigma M = 0·15$). Dissepiments are concentrated in bands 2 mm thick and approximately 5 mm apart.

In tangential section laminae occur as sheets of perforated tissue or zones of radial arms. The cross-section of pillars is circular, with their diameter smallest at the centre. The pillars are spool-shaped. The average number in 4 mm² for each coenosteum ranges between 17 and 24 ($M = 20·0$, $\sigma M = 2·0$, $\sigma m = 1·8$). An incipient astrorhizal system appears to be developed in one specimen. There are four specimens in this collection.

REMARKS: This species has thicker and more distantly spaced skeletal structures than any other described species of *Actinostroma* (Gr. στυλο = pillar, μεγα = large); the only species approaching the dimensions of *A. steloges* is *A. ingens* Ünsalander (1951) which should be removed to *Nexililamina* gen. nov. as mentioned in the discussion below.

Klovan (1966, p. 19, Pl. 4, fig. 1) described a species, *A. redwaterense*, which has a somewhat similar appearance to *A. steloges*, but the fewer number of pillars and laminae in 5 mm in vertical section

in *A. steloges* readily distinguishes it from *A. redwaterense*.

A. steloges is, however, very similar to the species described as *Gerronostroma concentricum* Yavorsky (1931). The microstructure of the holotype of the type species of *Gerronostroma* is in doubt, as no descriptions other than those of Yavorsky have been published, and he maintains that the tissue is compact. The paratype described by Galloway (1957) has fibrous tissue. If the tissue of *G. concentricum* is compact, then this new species may be synonymous with *G. concentricum*. The two species have very similar spacing and thicknesses of skeletal structures, and both occur in Couvinian strata.

RANGE: *A. steloges* occurs in the Couvinian Dip Creek Limestone Member of the Broken River Formation, 800 m SW. from its base, to the top of the Member on the Martin's Well traverse, 1 km south-west of Martin's Well (L.2982).

Nexililamina gen. nov.

TYPE SPECIES: *Nexililamina dipcreekensis* sp. nov.: holotype F.47608, from the base of the Dip Creek Limestone Member, Broken River Formation, 1 km SW. of Martin's Well, Pandanus Creek Station, North Queensland; Couvinian.

DIAGNOSIS: Coenostea are composed of well-developed pillars and laminae. Pillars are commonly continuous or continuously superimposed. Laminae may be composed of simple perforated sheets of compact tissue, or closely spaced system of microlaminae, forming a single complex lamina. Parts of coenostea show completely *Actinostroma*-like structure in vertical section. Radial arms joining pillars are not developed, but laminae in places are perforated. Astrorhizae are present.

REMARKS: This genus embraces those species which Lecompte (1951) placed in a group of *A. verrucosum*, and similar species which subsequently have been described. The genus is closely related to *Actinostroma*, and only differs in possessing complex combined laminae (L. *nexilis* = tied together, *lamina* = plate), the lack of radial arms, and the pillars frequently split beneath laminae which are widely spaced. In some parts of vertical sections of coenostea, the structure is completely analogous to that of *Actinostroma*. The holotype of the type species of *Actinostroma*, *A. clathratum*, shows some grouping of laminae but they always form simple sheets of hexactinellid network.

Atelodictyon Lecompte can be distinguished from *Nexililamina* by its discontinuous pillars confined to a single interlaminary space, and laminae which are composed of simple sheets of compact tissue arranged in an hexactinellid network.

Anostylostroma Parks also has pillars which are restricted to one interlaminary space, but the tissue of the laminae is not compact.

Species assigned to this genus include: *N. verrucosa* (Goldfuss) (1826) Couvinian to Frasnian; *N. mamontovi* (Yavorsky) (1955) Upper Couvinian to Lower Givetian; *N. mamontovi* var. *plana* (Yavorsky) (1955) Couvinian; *N. conglomerata* (Lecompte) (1951) Couvinian; *N. geminata* (Lecompte) (1951) Couvinian; *N. ingens* (Ünsalandcr) (1951) Frasnian; *N. dipcreekensis* sp. nov. Couvinian.

N. verrucosa has greater complexity of laminae than other species of this genus, and in parts the laminae have almost a cellular structure (see Lecompte 1951, Pl. 10, fig. 1a), and is tentatively referred to this genus.

Flügel (1959) has indicated that *N. conglomerata* and *N. geminata* do not conform to previously described genera.

Nexililamina dipcreekensis sp. nov.

(Pl. 14, fig. 4-8)

Actinostroma sp. Mallett in Hill, Playford & Woods 1967, p. d.4, Pl. D2, fig. 1a, b.

HOLOTYPE: F.47608, from the base of the Dip Creek Limestone Member, 1 km SW. of Martin's Well, Pandanus Creek Station, North Queensland; Couvinian.

DIAGNOSIS: Coenostea are globular, discoidal or encrusting. Laminae are compact with irregular undulations, 0·01 to 0·08 mm thick, and can be from 0·03 to 0·6 mm apart. There are alternating zones of closely spaced single laminae, and more widely spaced laminae which may be formed of several fused laminae. There is an average of 15 to 27 laminae in 5 mm in vertical section. Dissepiments are common and may extend laterally into microlaminae. Pillars are straight and continuous, 0·07 to 0·10 mm thick. They divide or break up into a number of strands beneath complex laminae. There are 20 to 27 pillars in 5 mm in vertical section, and an average of 20 to 30 in 1 mm^2 in tangential section. Astrorhizae have an axial canal 0·3 mm diameter with rare radiating canals.

DESCRIPTION: Coenostea are globular or discoidal with a diameter from 10 to 25 cm, but two specimens are laminar and encrusting, with low irregular mamelons 1 to 5 mm apart. Pillars are composed of compact tissue which appears to be commonly altered to the melanospheric or flocculent states. Laminae are composed of thin compact layers of tissue, 0·01 to 0·05 mm thick ($M = 0·034$, $\sigma M = 0·006$), which may occur separately or may be combined to form composite laminae. Composite laminae may be up to 0·08 mm thick. Where laminae are closely spaced they are simple, but where they are more widely spaced they are usually complex.

In vertical section laminae are continuous, lenticular, and have irregular undulations. The spacing of the laminae is not constant, and there may be as many as three in 1 mm, or they may be as far apart as 0·6 mm. There are alternating bands of closely and widely spaced laminae. The average number in 5 mm for each coenosteum ranges from 15 to 27 ($M = 23·5$, $\sigma M = 3·3$, $\sigma m = 1·8$). Dissepiments are common in the galleries and may be long and straight, developing into microlaminae. Pillars are straight and regular. They have a diameter of from 0·07 to 0·10 mm ($M = 0·089$, $\sigma M = 0·006$), and are slightly spool-shaped in some specimens. The

number in 5 mm ranges from 20 to 27 (M = 23·7, σM = 1·68, σm = 1·38). Pillars may split in interlaminary spaces, particularly where laminae are widely spaced; this is well illustrated in parts of the holotype. The splitting of pillars is also more common beneath complex laminae. Astrorhizal systems have an axial canal 0·3 mm diameter, and indistinct radiating canals. The laminae are upturned for a short distance around each system.

In tangential section laminae occur as thin sheets of compact tissue pierced by rare round pores 0·1 to 0·2 mm in diameter. The margins of the laminae rarely break down into a porous network, resembling crude radial arms joining pillars. Pillars are approximately circular in cross-section, and the average number in 1 mm² ranges from 20 to 32 (M = 26·4, σM = 2·7, σm = 1·9). Dissepiments composed of compact tissue cut across galleries, and join pillars. There are 19 specimens in this collection.

REMARKS: The only other species of this genus which has zones of closely and widely spaced laminae is *N. conglomerata* (Lecompte). The one Broken River species has more numerous laminae in 5 mm and they are occasionally lenticular.

RANGE: *N. dipcreekensis* is found through the whole of the Dip Creek Limestone Member (*derivatio nominis*) on the Martin's Well traverse, 1 km SW. of Martin's Well (L.2977, L.2979, L.2513, L.2981); and in the lower part of the Chinaman Creek Limestone Member, up to 140 m W. of the base of the Member on Chinaman Creek South (L.2509).

ACKNOWLEDGMENTS

This work is part of a study of the whole stromatoporoid fauna of the Broken River Formation on Pandanus Creek Station, done under the supervision of Professor D. Hill, and I would like to thank her for her assistance and encouragement. Dr. J. Jell made specimens available and also indicated suitable localities for making collections.

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APPENDIX:

DESCRIPTIONS OF COLLECTION LOCALITIES

DIP CREEK LIMESTONE MEMBER

MARTIN'S WELL TRAVERSE: SW. across the limestone from a point on the base of the limestone, 1 km SW. of Martin's Well, Pandanus Creek Station, with the distances of localities in a direction SW. from the base of the limestone.

L.2977—0-50 m (Couvinian)
L.2978—150 m (Couvinian)
L.2979—300 m (Couvinian)
L.2980—500 m (Couvinian)
L.2981—800 m (Couvinian)
L.2982—900 m (Couvinian)
L.2513—locality not on traverse, approximately

400 m SW. of the base of the limestone, 0·8 km SW. of Martin's Well. (Couvinian)

L.2499—Right-hand tributary of Pandanus Creek, 2·4 km upstream from the junction of Dip Creek and Pandanus Creek, 6 km E. of the homestead, Pandanus Creek Station. (Couvinian)

L.2984—Ridge, 165 m NE. of creek crossing. 6·8 km S. of the Pandanus Creek Homestead on the Pandanus Creek-Wandovale Road. (Couvinian or Lower Givetian)

Isolated Rudites

L.2968—Wandovale-Pandanus Creek Road, 2·8 km S. of Pandanus Creek Homestead. (Couvinian)

Chinaman Creek Limestone Member

Traverse up Chinaman Creek South: Distances are measured W. from the base of the limestone member.

L.2509—140 m (Couvinian)

L.2510—500 m (Givetian)

L.2976—1,000 m (Givetian)

DESCRIPTION OF PLATES

Plate 13

Fig. 1—*Actinostroma papillosum* (Bargatzky), vertical section, × 10. F.47635 from the top of the Chinaman Creek Limestone Member on Chinaman Creek South, Pandanus Creek Station (Givetian).

Fig. 2—*Actinostroma clathratum* Nicholson, vertical section, × 10. F.47591 from 150 m SW. of the base of the Dip Creek Limestone Member, 1 km SW. of Martin's Well, Pandanus Creek Station (Couvinian).

Fig. 3—*Actinostroma dehornae* Lecompte, tangential section, × 10. F.47874 from 500 m W. of the base of the Chinaman Creek Limestone Member, Chinaman Creek South, Pandanus Creek Station (Givetian).

Fig. 4—*Actinostroma clathratum* Nicholson, tangential section, × 10. F.47982 from Chinaman Creek Limestone Member on Chinaman Creek South, Pandanus Creek Station.

Fig. 5—*Actinostroma dehornae* Lecompte, vertical section, × 10. F.47874.

Fig. 6, 7—*Actinostroma stellulatum* Nicholson. F.42688B from Dip Creek Limestone Member on Dip Creek, 2·4 km upstream from the junction of Dip Creek and Pandanus Creek, Pandanus Creek Station (Couvinian). 6. tangential section, × 20. 7. vertical section, × 10.

Plate 14

Fig. 1-3—*Actinostroma steloges* sp. nov. Holotype, F. 47755, from Dip Creek Limestone Member of the Broken River Formation, 800 m SW. of the base of the Member, 1 km SW. of Martin's Well, Pandanus Creek Station. 1. vertical section, × 20, showing coarse skeletal elements with impersistent laminae. 2. vertical section, × 10, showing the coarse continuous pillars. Alteration has affected the specimen in the central part of the figure. 3. tangential section, × 10, showing radial arms joining pillars and some pillars with dark lumen.

Fig. 4-8—*Nexililamina dipcreekensis* sp. nov. 4. vertical section, × 10, F.47741, from the Dip Creek Limestone Member, 500 m SW. of its base, 1 km SW. of Martin's Well, Pandanus Creek Station; showing a typical astrorhiza. 5. tangential section, × 10, Holotype, F.47608, from the base of the Dip Creek Limestone Member 1 km SW. of Martin's Well, Pandanus Creek Station; showing laminae as porous sheets of compact tissue with no radial arms joining pillars. 6. vertical section, × 20, Holotype, showing a part of the coenosteum where pillars split beneath laminae, and a complex lamina is formed by the fusion of two laminae. 7. vertical section, × 50, Holotype, showing fine simple laminae with thicker pillars. The tissue of the pillars has light spots which are not considered to be vacuoles, but imperfections in preservation. Many specimens are excellently preserved and the tissue is in the main compact. 8. vertical section, × 10, Holotype. This section shows simple and complex laminae, closely and distantly spaced. The lower part of the section is oblique to the pillars and gives a false impression that pillars are short and confined to a single interlaminary space.